Original Articles

Tropical stream diatom communities – The importance of headwater streams for regional diversity

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ABSTRACT

Understanding how species are distributed in space and time is a focal element guiding conservational efforts under ongoing climate change and the Holocene extinction. Freshwater habitats are currently one of the most threatened ecosystem types, and studies aiming to unravel factors that govern biodiversity of tropical stream micro-organisms are especially scarce. Diatoms play an important role as primary producers in streams and are widely used as ecological indicators. However, relatively little is known about which factors affect diatom communities in the tropics.

Here, we studied benthic diatom diversity across 67 tropical streams spanning stream orders 1–5 in Kenya. We examined whether the hypothesis of latitudinal diversity gradient applies for benthic diatoms, i.e. whether tropical streams encompass more species than boreal streams using a comparable boreal dataset. In addition, we studied which environmental, land use and spatial factors control benthic diatom communities using redundancy analysis. We also examined the nestedness and turnover components of beta diversity, factors contributing to diatom species richness, and the uniqueness of the communities across stream orders by using boosted regression trees and local contribution to beta diversity. Finally, we studied whether environmental heterogeneity and beta diversity are related across stream orders and tested their relationship using tests of homogeneity of dispersion and regression analysis.

Species richness was not higher in tropical streams than in boreal ones. Tropical diatom communities were controlled jointly by local environmental and spatial factors. Although water chemistry was the most important controlling factor, also physical variables contributed significantly to community variation. Land use had also a significant effect on diatom communities as broad leaved forest streams harboured different diatom communities compared with streams with higher human impact and conductivity, stressing the importance of forests to water quality and diatom biodiversity. Headwater streams encompassed the highest species turnover, whereas nestedness was higher in higher order streams. Species richness was significantly higher in higher order streams than in headwaters, whereas the uniqueness of the communities peaked in headwaters. Environmental heterogeneity was the highest in headwater streams and was related to high beta diversity, which highlights the importance of habitat heterogeneity to biodiversity. Our results stress the management and conservational importance of headwater streams and tropical montane forests as these environments harbour unique diatom communities important for regional diversity.

1. Introduction

How species are distributed across the Earth in space and time remains a fundamental topic guiding conservation efforts under ongoing climate change and the Holocene extinction (Pimm et al., 1995; Thomas et al., 2004). The extinction threat concerns not only terrestrial ecosystems but also aquatic communities. Freshwater habitats harbour a disproportionately large species richness in relation to habitat area in many taxonomic groups and freshwater biodiversity is more threatened than biodiversity in other ecosystems (IUCN, 2009; Strayer and Dudgeon, 2010; Wiens, 2016). Thus, an understanding of the drivers that maintain species diversity is urgently needed in order to combat the severe biodiversity losses taking place at the present.

While studies aiming to unravel the determinants of macro-organismal biodiversity have been extensive (Rosenzweig, 1995), microbial communities (e.g. bacteria, unicellular algae and fungi) have received

less attention in this regard (Green et al., 2004; Zeglin, 2015). For example, whereas latitudinal diversity gradients are well documented for macro-organisms (Gaston, 2000; Hillebrand, 2004; Lawton, 1999), the existence of such a pattern for micro-organisms remains a controversial issue (Hillebrand and Azovsky, 2001; Passy, 2010; Salinas et al., 2015). Furthermore, microbial biodiversity studies in boreal and temperate regions have been far more numerous than in the tropics but see for example (Bellinger et al., 2006; Bere, 2014; Bojorge-Garcia et al., 2014; Mangadze et al., 2015).

The diversity and composition of microbial communities are affected by a wide range of determinants and there is still no consensus as to whether the key drivers are more related to the local environment (Gothe et al., 2013; Maloufi et al., 2016) or spatial factors (Crump et al., 2007; Soininen et al., 2004). Also land use (Bere and Tundisi, 2011; Carpenter and Waite, 2000) or climatic factors (Pajunen et al., 2016) may affect aquatic microbial communities. Finally, the spatial scale of the study influences the factors which govern microbial communities (Lindstrom and Langenheder, 2012), and communities may thus often be described by the shared influence of spatial and environmental factors, with increasing spatial influence in larger studies (Heino et al., 2014; Soininen et al., 2016; Verleyen et al., 2009).

Freshwater organisms may be especially vulnerable to changes in precipitation and possible droughts can quickly alter a freshwater habitat and thus its biodiversity (Wiens, 2016). Streams encompass a disproportionately high biodiversity (Vinson and Hawkins, 1998; Vorosmarty et al., 2010), and the stream network provides an excellent environment to study diversity patterns via its hierarchic dendritic organization (Grant et al., 2007). The river continuum concept (RCC) predicts biological diversity to peak at mid-order streams, whereas headwaters and large rivers should be less diverse (Vannote et al., 1980). However, while this prediction might hold true for alpha (local) diversity, beta (between-site) and gamma (regional) diversity may show different patterns as especially headwater streams (orders 1–2) may harbour a greater proportion of biodiversity compared with higher order stream branches (Meyer et al., 2007). Moreover, human induced disturbances usually increase with increasing stream order (Januchowski-Hartley et al., 2011), which may affect biodiversity. Headwater streams may also be more physically variable promoting environmental heterogeneity and subsequently also beta diversity (Finn et al., 2011). Consequently, possible environmental homogenization in higher order streams may decrease beta diversity compared with headwaters.

High beta diversity in headwaters may also be caused partly by the more isolated position of headwater streams compared with higher order branches (Finn et al., 2011). Thus, highly connected sites at lower reaches harbour lower beta diversity due to a higher exchange of individuals between sites leading to homogenisation of communities (Lopes et al., 2014). Furthermore, anthropogenic and natural stressors may cause different patterns in beta diversity given that beta diversity under natural disturbances may be caused more by species turnover (i.e. the shared number of species between sites is small), whereas community dissimilarities under anthropogenic stressors may be more generated by nestedness (i.e. poorer assemblages are subsets of those of richer sites) (Gutierrez-Canovas et al., 2013). These patterns are largely unresolved in the tropics, however, as stream beta diversity has not been studied extensively in tropical regions (but see Al-Shami et al., 2013; Tonkin et al., 2016) and microbial communities have received even less attention.

Sub-Saharan Africa is going through an intense land cover change due to human population growth and the subsequent conversion of forests into arable land (Brink et al., 2014; Pellikka et al. 2018). Land cover changes can have severe effects on the environment and natural resources (Alcantara-Ayala et al., 2006; Hohenthal et al., 2015). Furthermore, land use changes in the catchments may have profound effects also on aquatic ecosystems via water scarcity, increased turbidity, and nutrient fluxes (Allan and Castillo, 2007; Hohenthal et al., 2015;

Soininen et al., 2015). The human impact on stream communities usually increases downstream, agricultural effects being the most severe threat to biodiversity (US -Environmental Protection Agency, 2000; Vorosmarty et al., 2010). The detrimental anthropogenic effects are increased by poor waste water treatment in many rural areas (Concoran et al., 2010). Indeed, freshwater biodiversity conservation under the increasing human demands for water poses a true challenge (UNESCO, 2009; Wiens, 2016; Vorosmarty et al., 2010).

Benthic diatoms are a pivotal component of stream biodiversity and are widely used as ecological indicators (Hill et al., 2000; Wang et al., 2005). We studied the diversity and composition of stream benthic diatom communities in the Taita Hills, Kenya. The area is considered a biodiversity hotspot with a high rate of endemism of plants (Beentje and Ndiang'ui, 1988; Gereau et al., 2006; Lovett and Wasser, 1993) and animals (Gereau et al., 2006). At the same time, however, the area is affected by intensive land use change along with other anthropogenic pressures threatening ecosystems and their functioning (Pellikka et al., 2013; Pellikka et al., 2009). First (Q_1), we were interested in whether there are major richness differences between tropical and boreal stream diatoms. We thus compared diatom species richness between tropical and boreal streams using two data sets with identical sampling methods. We expected that species richness would be higher in the tropics as found for other taxa (Hillebrand, 2004). Second (Q_2), we studied the effects of local environmental, land use and spatial factors on tropical stream diatom community composition. We expected water chemistry and stream physical variables to have a significant effect on diatom composition (Soininen, 2007) but also that communities are spatially structured (Piano et al., 2017). In addition, we expected land use to affect diatom communities indirectly via affecting water quality (Bere and Tundisi, 2011; Carpenter and Waite, 2000; Potapova and Charles, 2002). We considered the use of diatom diversity as an ecological indicator of land cover change by sampling diatoms in four massifs of the Taita Hills of Kenya, which differ in their land use history but are similar in their bedrock, soil types, forest species composition, agricultural crop composition and climate. Third (Q_3), we studied the distribution of diatom biodiversity across stream orders. We expected headwater sites (orders 1–2) to harbour more unique diatom communities and, simultaneously, to have lower species richness than higher stream order sites (Meyer et al., 2007; Sherwood et al., 2000). We also examined beta diversity components, i.e. species turnover and nestedness across stream orders, and expected species turnover to be largest in headwaters while nestedness is largest in downstream sites. Fourth (Q_4), we examined factors contributing to diatom species richness and the uniqueness of the communities. We expected that species richness is mostly related to conductivity (Heino et al., 2010) and pH (Jyrkankallio-Mikkola et al., 2017), whereas uniqueness would be most related to conductivity and nutrient levels (Pajunen et al., 2017). Finally (Q_5), we studied whether environmental heterogeneity and diatom beta diversity are related across stream orders and tested their relationship. We expected headwater streams to harbour higher beta diversity and environmental heterogeneity (Finn et al., 2011; Meyer et al., 2007) than sites at higher order streams.

In this study, we characterized diatom communities using species richness, community composition and the uniqueness of species composition at sites, measured as local contribution to beta diversity (LCBD) (Legendre and De Caceres, 2013). Since beta diversity provides the most useful measure to understand the processes that generate and maintain biodiversity (Legendre et al., 2005; Qiao et al., 2015; Socolar et al., 2016) we placed most emphasis on beta (between site) diversity in terms of dissimilarities and LCBD.

2. Material and methods

2.1. Study area

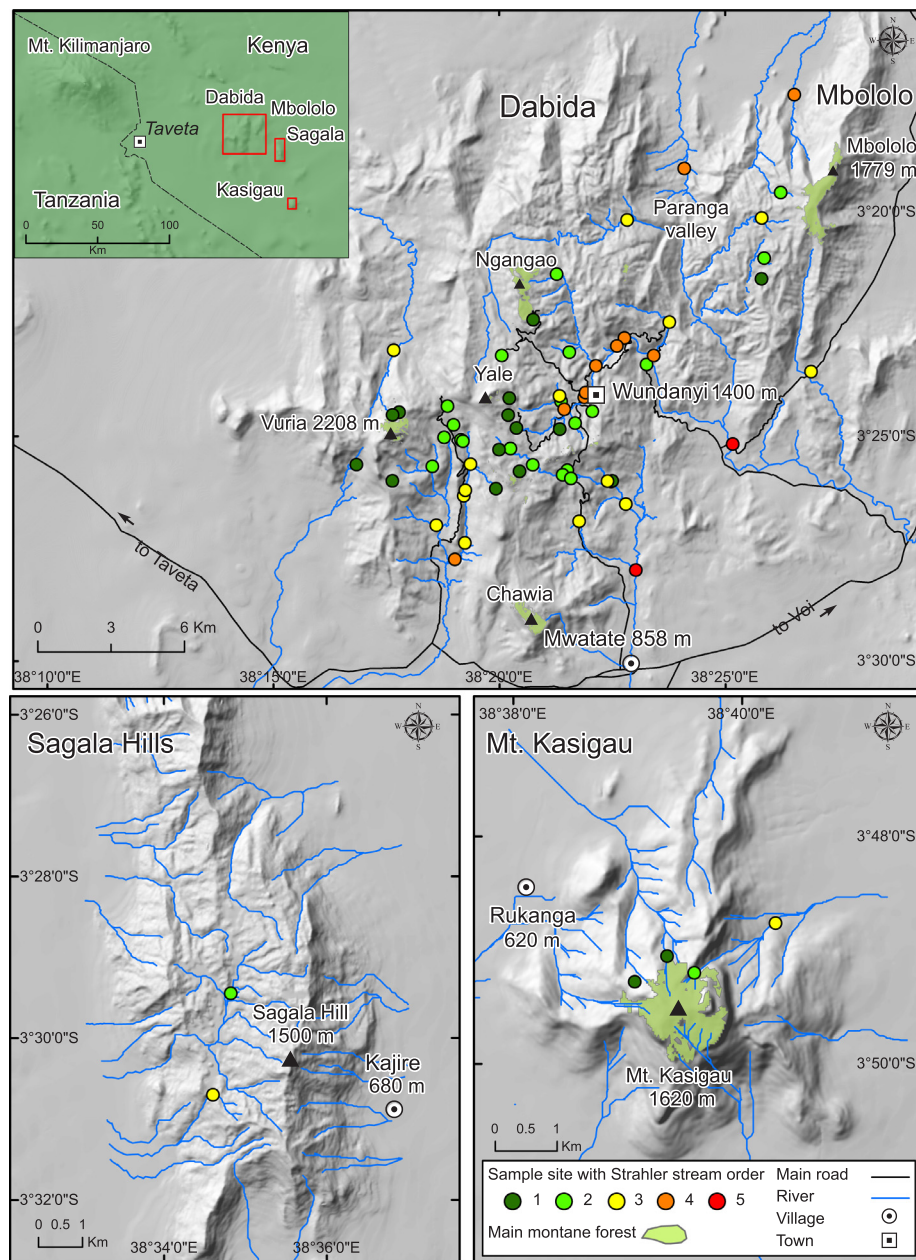The Taita Hills form the northernmost part of the biodiversity

Fig. 1. Map of the sampling area.

hotspot, the Eastern Arc, located in south-eastern, Kenya rising in the middle of the plains to hilltops with an altitude of over 2000 m (Platts et al., 2011). The Taita Hills can be separated into the Dabida massif, Mbololo massif, Sagala Hill and Mt.Kasigau, which are within 40 km off each other. The mean elevation of Dabida is between 1300 and 1600 m a.s.l., the highest peaks reaching over 2000 m a.s.l. Mbololo massif, which reaches 1800 m, is located east of Dabida and is separated by the Paranga valley at 900 m a.s.l. Sagala Hill, which reaches 1500 m a.s.l., is located 15 km south-east off Dabida and Mbololo, and Mt.Kasigau, which reaches 1600 m a.s.l., is located 40 km south-east off Dabida (Fig. 1). Located in the intertropical convergence zone, the Taita Hills face a bimodal rain pattern with a rainy season in November–December and March–May. Annual rainfall in the hills is normally 1200 mm, while the lowlands receive < 600 mm per year, agreeing with the rule of thumb that higher elevations have higher rainfall and are covered more by forests than lower elevations (Erdogan et al., 2011). However, as the rains are orographic in nature, the eastern slopes and hills of Mbololo and Dabida receive more precipitation than the leeward parts

and slopes located in the west. A significant addition to the precipitation is occult precipitation, which is estimated to result in a 20% addition to precipitation, but only in the forests as forest volume is required to capture the atmospheric moisture, the mist (Pellikka et al., 2018).

It is estimated that the hills over approximately 1220 m a.s.l. prior to human disturbance were covered by forests characterized as evergreen moist lower or upper montane forests. Now only a few per cent of the montane forests are left, mainly as protected forests managed by the Kenya Forest Service. Below 1220 m a.s.l. the forests can be characterized as Acacia–Commiphora woodland, which is partly deciduous depending on the species. The hills are cleared for intensive small-scale agriculture, the main crop being maize producing to harvest each year (Jaetzold and Schmidt, 1983). The lowlands are used for dryland farming, grazing by goats and camels, sisal plantations and conservation areas.

The four massifs studied differ in their land use. Based on Pellikka et al. (2018), only the hilltops of the Dabida and Mbololo massifs are

covered by montane forests. Due to cloudy conditions, the peak of Vuria (2208 m a.s.l.) is characterized as upper montane forest, elfin forest, with trees covered heavily by epiphytes (Stam et al., 2017), while the other native forests are lower montane forests with less epiphytes but trees reaching up to 40 m in height. Over 1220 m a.s.l., covering an area of 241 km^2, croplands cover nowadays 40.4%, montane forests 3.2% plantation forests of mainly pine and eucalyptus 10.1%, and woodland, shrubland and thickets all together 44.8% (Pellikka et al., 2018). The remaining fragments of montane forests in the Dabida and Mbololo massifs are 1–2 km^2 in size: Mbololo (185 ha), Ngangao (120 ha), Vuria (64 ha) and Chawia (86 ha) being the largest ones. These forests are all degraded due to selective timber harvesting and grazing inside the forest, especially in Vuria and Chawia. The least degraded is Mbololo forest and then Ngangao (Omoro et al., 2013).

Sagala Hill has no native montane forests left, but it has some plantation forests and degraded woodlands. The montane forest of Mt.Kasigau can be characterized as upper montane forest over 1500 m a.s.l. due to misty conditions producing fog deposit, and lower montane forest down to 1000 m a.s.l. (Medley and Maingi, 2014) below which dryland forest like Acacia-Commiphora with Euphorbia ssp. is found. The montane forest of Kasigau is the least disturbed of all the forests of the Taita Hills, being 2.03 km^2 in size (Medley and Maingi, 2014). Croplands did exist in Mt.Kasigau a few decades ago but were abandoned in order to safeguard water resources (Rikkinen et al., 2015). Evidently due to very steep slopes they were also difficult to manage (Adhikari et al., 2017).

2.2. Biological data collection

Diatom samples were collected at 67 sites from the four massifs (Fig. 1). Sampling was completed in three weeks in January 2016. Diatoms were sampled by randomly selecting and brushing 10 cobble-sized stones or bedrock. The samples were collected from different parts of the stream site in order to control small-scale variability in community composition. To standardize the sampling area we used a 5 × 5 cm rubber template. The samples were preserved with 99% ethanol and stored at +4 °C. Wet combustion with hydrogen peroxide (20%, H_2O_2) was used to clean diatom frustules from organic material. Subsequently, samples were mounted on microscope slides using the high-refractive mounting resin Naphrax. We counted and identified at least 500 frustules from each sample using phase contrast light microscope with 1000× magnification. Species identification was based on Krammer and Lange-Bertalot (1986–1991) and Taylor et al. (2007).

2.3. Chemical and physical measurements

Water samples for total nitrogen, total phosphorus and water colour were collected a few metres upstream from each sampling site. Total nitrogen was determined by using alkaline persulfate digestion where alkaline oxidation is carried out in a thermo digester and the converted total nitrogen quantified colorimetrically. Total phosphorus was determined by inductively coupled plasma-optical emission spectrometry (ICP-OES). However, as the method lacked the sensitivity to determine phosphorus concentrations below 10 µg L^{-1} and the phosphorus content of 51 samples was ≤ 10 µg L^{-1} we were unable to use total phosphorus in the following analyses. Water colour was analysed using the standardized method (EN ISO7997).

To measure conductivity, pH and temperature in the field we used a YSI Professional Plus water quality meter (YSI Inc., Yellow Springs, OH, USA). Current velocity was measured with a Schiltknecht MiniAir-2 flow meter (Schiltknecht, Gossau, Switzerland) from 30 locations covering the sampling site extensively. Water depth was similarly measured from 30 locations and stream width from 10 locations covering the length of the whole sampling site.

Substratum particle size was measured from 10 locations using a 50 × 50 cm quadrat placed in random sites on the stream bed. We used

a modified Wentworth scale to visually classify the substratum particle size: sand (diameter 0.25–2 mm), gravel (2–16 mm), pebble (16–64 mm), cobble (64–256 mm) and boulder (> 256 mm) (Wentworth, 1922). Canopy shading was individually estimated from 20 locations covering the whole sampling site. Table containing the average values of measured environmental variables excluding land use variables that were calculated to independent sites are listed in Appendix- A in the Supplementary Material.

2.4. Stream order analyses and land cover data

River network and stream ordering were calculated from digital elevation model (DEM) data. A DEM of 1 × 1 m resolution was derived from airborne laser scanning (ALS) data sets for two parts of the study area (the Taita Hills and Kasigau). Laser scanning data were acquired in 2013 and 2014 (using an Optech ALTM 3100 laser scanner), and the data were filtered for buildings, powerlines and outliers using Terrascan software (Terrasolid Oy, Finland), LAStools (Rapidlasso GmbH, Germany) and manual editing. For the Sagala area, a DEM was created from a scanned Survey of Kenya 1:50000 scale topographic map from which the contour lines were digitized and converted to a 10 m resolution raster DEM.

Watershed delineation was based on the DEM layers and, hydrological modelling tools in ArcGIS 10.3.1. First, elevation grids were filled to create a surface that has no sinks. Then, a flow direction grid was calculated to determine the direction of flow for each cell in the landscape. A flow accumulation function was used to generate a drainage network for the selected pour points. The Snap Pour Point tool was used to ensure selection of points of high accumulated flow, and finally watersheds were automatically delineated. ArcGIS 10.3.1 hydrological tools and Stream Order function with the Strahler method (Stahler, 1957) were used to determine stream ordering from the river networks. Elevation models were harmonized by resampling the DEM layers into 10 m pixel size. River networks were then determined again and stream ordering calculated.

Land cover was assessed from classified satellite imagery separately for the Taita Hills, Kasigau and Sagala. For the Taita Hills, the land cover classification was based on a 20 × 20 m resolution SPOT 4 satellite image from 23-October 2011 (CNES, 2013). The satellite image was classified into nine land cover classes (Heikinheimo, 2015; Appendix- A, sheet for land use in the Supplementary Material) using an object-based approach (Benz et al., 2004) following the methodology presented in Clark and Pellikka (2009). Segmentation and classification were implemented in the eCognition software (Trimble). After manual corrections, the overall accuracy of the land cover map was 71.1% when comparing the map with 305 random ground-truth points.

For the Sagala area, a Sentinel-2A MSI Level-1C satellite image from 8-October 2016, downloaded from the Sentinel's Scientific DataHub (ESA, 2015), and the RandomForest (Breiman, 2001) classifier in R software were used to create the land cover classification. First, a DOS1 atmospheric correction was applied to the Sentinel-2A data using the Semi-Automatic Classification Plugin in QGIS. Then, classifier training areas were on-screen digitized from a very high-resolution (1m pixel size) image mosaic from 2004 and from more up-to-date satellite imagery (Google Earth, 2017). Then, reflectance values from the four bands – blue, green, red and infra-red – from the Sentinel–2A satellite image were used as the predictors for the RandomForest classifier. The image was classified into the following relevant classes: bush, fields, forest and impervious.

For the Kasigau area, information from the same Sentinel–2A satellite image was combined with a canopy height model (CHM) and DEM derived from the ALS data for creating the land cover classification map. First, the CHM was reclassified into five elevation classes in ArcGIS 10.3.1. normalized difference vegetation index values derived from the Sentinel-2A satellite image were used to separate non-vegetated areas from different types of green areas. Then, the Kasigau study

area was classified into highland and lowland zones based on the 1 m pixel size DEM to separate montane vegetation from lowland vegetation after which ArcGIS Map Algebra tool was used to derive the land cover classes listed in Appendix- A in the Supplementary Material. The resulting land cover map was evaluated using GPS field measurements, very high resolution airborne imagery (1m pixel size) and also previous knowledge of the area. Prior to statistical analyses, the land cover classes of the six sampling sites from Sagala and Kasigau were equated with those classified from the Taita Hills. Finally, zonal statistics of the percentages of land use and land cover classes were calculated for different watershed areas based on the land cover layers and delineated watersheds for the whole study region.

2.5. Statistical analyses

Prior to analyses, explanatory variables measured as percentages were arcsine- transformed, while other explanatory variables were log-transformed. In addition, diatom abundance data were Hellinger transformed to better meet the requirements of linear ordination methods (Legendre and Gallagher, 2001). Correlations between explanatory variables were tested using Pearson correlation. As none of the correlations exceeded 0.70, we kept all the explanatory variables in the subsequent models (Dormann et al., 2013).

Failure to notice spatial autocorrelation can lead to false interpretations of the effects of environmental variables on community composition. Thus, spatial autocorrelation of the local environmental variables and species richness was tested using the function correlog in the R package 'pgirmess' (Giraudoux, 2015). The significance of the correlogram was tested at level $P \le 0.05$ with an applied Bonferroni correction (P/k, where k is the number of distance classes used). Here, the distance class of 7 km was used as it was most suitable for the spatial distances in our data.

To test whether more species are found from the tropical than boreal areas (Q_1), species accumulation curves (function specaccum in the R package 'vegan'; (Colwell and Coddington, 1994; Palmer, 1990)) were used. The used boreal stream diatom data are explained in detail in Jyrkankallio-Mikkola et al. (2017). To standardize the number of sampling sites, 67 samples from the boreal data, originally comprising 105 sites, were chosen. The first order Jackknife method was used to estimate the total species richness for both biomes.

To model spatial structures among tropical study sites, distance-based Moran's eigenvector maps (dbMEM) derived from spatial coordinates (function dbmem in the R package 'adespatial'; (Dray et al., 2017)) were used. The threshold value was calculated using the function give.thresh. Only eigenvectors with positive autocorrelation were used to model spatial effects in subsequent analyses.

Redundancy analysis (RDA) was applied to study community structure (abundance data) and -environment (excluding land use) relationships (Q_2) for the whole tropical data set (Legendre and Legendre, 2012). Another RDA was conducted exclusively for 39 independent sites (i.e. sites that had independent catchments) to examine the effects of land use and catchment size on the diatom communities. A stepwise model (forward selection) with 200 permutations was used to create final RDA models (function ordiR2step in the R package 'vegan'; (Oksanen et al., 2015)).

Distribution of biodiversity across stream orders (Q_3) was studied with a set of analyses. To study the uniqueness of diatom community composition across sites, LCBD was calculated for each site (function beta.div in the R package 'adespatial'; (Legendre and De Caceres, 2013)). The analysis was based on abundance data on which the Hellinger dissimilarity coefficient was applied and the analysis was run with 999 permutations. Linear regression was applied to study the relationship between species richness and LCBD across sites and how richness and LCBD varied across stream orders. To study whether different dissimilarity components govern diatom beta diversity across stream orders, total beta diversity (β_{sor}), species turnover (β_{sim}) and

nestedness (β_{nes}) were calculated for two groups of stream orders, 1–2 and 3–5, respectively (function beta.multi in the R package 'betapart' (Baselga et al., 2017)). These components were calculated using following equations:

$$\beta_{sor} = \frac{b + c}{2a + b + c},$$

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)},$$

$$\beta_{nes} = \beta_{sor} - \beta_{sim}$$

where *a* is the number of species found at both sampling sites, *b* is the number of species found at the first site but not at the second site and *c* is the number of species that are found at the second site but not at the first site (Baselga, 2010).

To explain variation in species richness and LCBD using environmental variables (Q_4), boosted regression trees (BRT; function gbm.step in R package 'dismo', (Elith et al., 2008; Hijmans, 2015)) were used. This function assesses the optimal number of boosting trees using k-fold cross validation. The function divides the data into 10 subsets and fits a gbm model of increasing complexity along the sequence. The function calculates the residual deviance at each step after which the function calculates the average holdout residual deviance and its standard error and then identifies the optimal number of trees as that at which the holdout deviance is minimised (Hijmans, 2015).

Ideal tree complexity was tested through tree complexities 1–4 and running the analysis 10 times with each setting (Appendix- B in the Supplementary Material). In the chosen model a Poisson distribution of error was used for species richness and Gaussian for LCBD. In both models, tree complexity was set to 3, learning rate to 0.001 and bagging fraction to 0.75. The benefits of this machine learning technique include, that it can be run with raw values, it takes into account interactions between predictors and has small prediction errors (Elith et al., 2008).

A test of homogeneity of dispersion (PERMDISP, function betadisper in the R package 'vegan' (Anderson, 2006; Anderson et al., 2006)) was applied to relate environmental heterogeneity (habitat variables) within stream orders to corresponding variation in diatom community composition (Q_5). The Sørensen coefficient was used for presence-absence data and Euclidean distances were applied for standardized habitat variables. PERMDISP–analysis tests among group differences from individual observation to their group centroid using ANOVA F-statistics (Anderson et al., 2006). The null hypothesis that there is no difference in diatom beta diversity and environmental heterogeneity among the different stream orders was tested. All tests were run using 999 permutations. Finally, the null hypothesis that there is no relationship between the degree of beta diversity and the degree of environmental heterogeneity across the different stream orders was tested using linear regression.

Explained variation in RDA and linear regressions were reported using adjusted R^2- values. All analyses were conducted in R version 3.2.2 (R Development Core Team, 2013) using packages ´adespatial' (Dray et al., 2017), ´betapart´ (Baselga et al., 2017), 'corrplot' (Wei and Simko, 2016), 'dismo' (Hijmans, 2015), 'pgirmess' (Giraudoux, 2015) and 'vegan' (Oksanen et al., 2015).

3. Results

Altogether 297 taxa were identified from 67 tropical sites, with 104 found at only one site. Local diatom species richness varied from 15 to 71 in the tropical data set. The random selection of 67 sampling sites from a comparative boreal data set resulted in a taxa richness of 303. Species accumulation curves revealed that there was only a minor difference in the proportion of total species richness for the boreal (76.4%) and tropical (74.6%) data sets (Q_1; Appendix- C in the
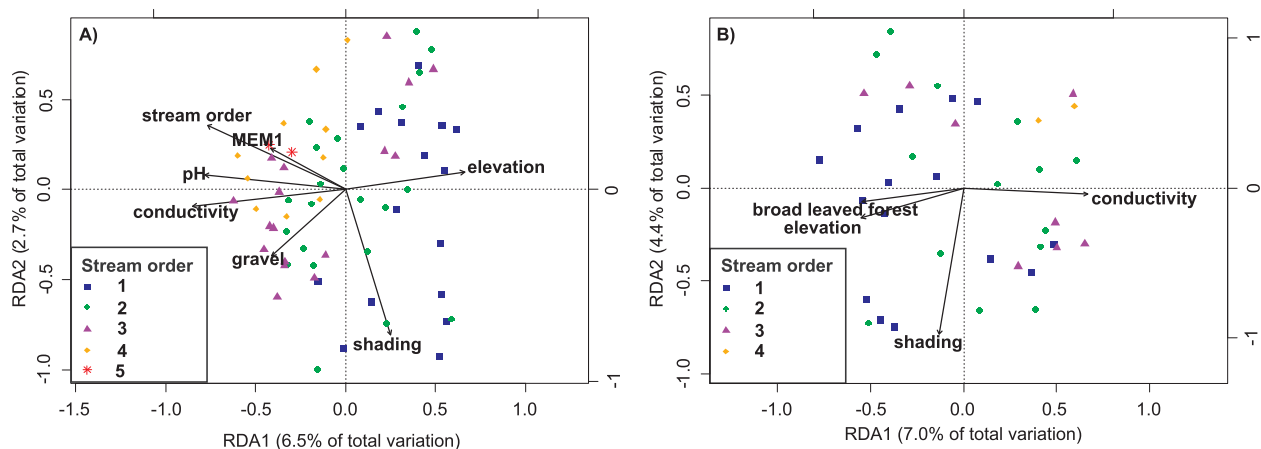
Fig. 2. Ordination plots for redundancy analysis for (A) all 67 sampling sites and environmental variables and (B) for 39 sites with independent catchment areas and environmental and land use variables. Both ordination plots are based on Hellinger transformed diatom abundance data. Arrows represent the significant environmental variables. The explained variation is based on adjusted R^2. Abbreviations: MEM1 (spatial eigenvector derived from distance-based Moraṅs eigenvector maps).

Supplementary Material).

Of the local environmental variables, only water temperature and stream width showed significant spatial autocorrelation over short distances (Appendix- D in the Supplementary Material). Species richness showed no spatial autocorrelation. dbMEM returned one spatially autocorrelated eigenvector (referred to henceforth as MEM1), which was used to model spatial structures among sites in the subsequent RDA and BRT analyses.

In the first RDA (67 sites), a forward selection method returned seven significant ($P < 0.05$) variables which together explained 15.6% of the total community variation (Q_2, Fig. 2a). Conductivity and pH were among the most important variables for diatom composition. Also the physical variables (shading and gravel), spatial (elevation and MEM1) and stream order were among the significant variables structuring the community. The first RDA- axis divided the sites with high conductivity, pH and high stream order opposite to those with high elevation. The second RDA- axis was mostly related to shading. We further tested whether removing singletons would increase the explained variation in community composition. This resulted only into a minor increase (15.9%) in the explained variation with the same explaining variables. When presence–absence data were used, explanatory power decreased to 10.9%. In the second RDA (39 sites) including land use variables, the selection method returned four ($P < 0.05$) significant variables which explained 14.4% of the total community variation (Q_2, Fig. 2b). The first RDA- axis divided the sites with a high percentage of broad leaved forest and high elevation opposite to those with high conductivity.

According to linear regression, species richness increased significantly with increasing stream order (Q_3, Fig. 3a, $P < 0.001$, $R^2 = 0.142$), whereas LCBD values showed an opposing trend with the highest values in headwater streams (Q_3, Fig. 3b, $P < 0.05$, $R^2 = 0.053$). LCBD and species richness showed a significant negative relationship (Q_3, Fig. 3c; $P < 0.001$, $R^2 = 0.425$). Total beta diversity was higher in headwater streams (Q_3, orders 1–2, $\beta_{sor} = 0.933$) than in higher order streams (orders 3–5, $\beta_{sor} = 0.867$). Beta diversity components varied across stream orders. As we expected, species turnover was higher in headwater streams (orders 1–2, $\beta_{sim} = 0.905$) than in higher order streams (orders 3–5, $\beta_{sim} = 0.860$), whereas nestedness was lower in headwater streams ($\beta_{nes} = 0.027$) than in higher order streams ($\beta_{nes} = 0.036$).

In the BRT analysis, the most important factors affecting species richness were temperature, pH and conductivity (Q_4, Fig. 4a). The most important variables affecting LCBD were conductivity, temperature and water colour (Q_4, Fig. 4b). Fitted function curves and scatter plots

arrived from the models for these variables are presented in Appendix-E.

PERMDISP revealed that there were significant differences in the degree of beta diversity ($P < 0.01$, F = 6.55) and environmental heterogeneity ($P < 0.05$, F = 3.30) among the stream orders (Q_5, Fig. 5a, b). Beta diversity and environmental heterogeneity were higher in headstreams than in higher order streams (Q_5, Fig. 5a, b). Albeit based on only five observations, we found a significant positive relationship ($P < 0.05$, $R^2 = 0.736$) between the degree of beta diversity and environmental heterogeneity.

4. Discussion

Tropical studies focusing on diatom community structure, species richness and beta diversity patterns and their underlying processes are still rare compared with temperate and boreal studies. In addition, diatom diversity patterns along stream networks are also generally relatively poorly understood. Here, our results shed light on the patterns and controlling factors of these important and understudied issues and may be relevant for watershed management and biomonitoring.

Even if largely similar sampling methods and efforts were used, we revealed no clear differences in diatom species richness between tropical and boreal areas (Q_1). As the sampling area of the boreal data set was larger than the tropical, and as species richness usually increases with the size of the sampling area, we further tested the difference in species richness between boreal and tropical areas by choosing only the 67 southernmost sites of the boreal data set in order to have more comparable sampling areas. This approach resulted in a total species richness of 298 in the boreal data set and a proportion of total species richness on the species accumulation curve of 77.9%, which indicates that tropical and boreal streams seem not to differ in diatom species richness. Earlier literature about latitudinal diatom richness patterns have documented very variable richness gradients. Passy (2010) found the relationship of benthic diatom richness and latitude to be U-shaped in a study that comprised running waters of the continental U.S.A. Highest species richness was found from subtropical and temperate sampling sites and was related to nutrient resources rather than climate. A positive relationship between marine diatom species richness and decreasing latitude was found by Salinas et al. (2015), whereas Hillebrand and Azovsky (2001) found no latitudinal effect for diatom species richness and suggested that latitudinal diversity gradient is determined by body size. Hence, our results add to the controversy of the subject and call for further investigation in different types of ecosystems.
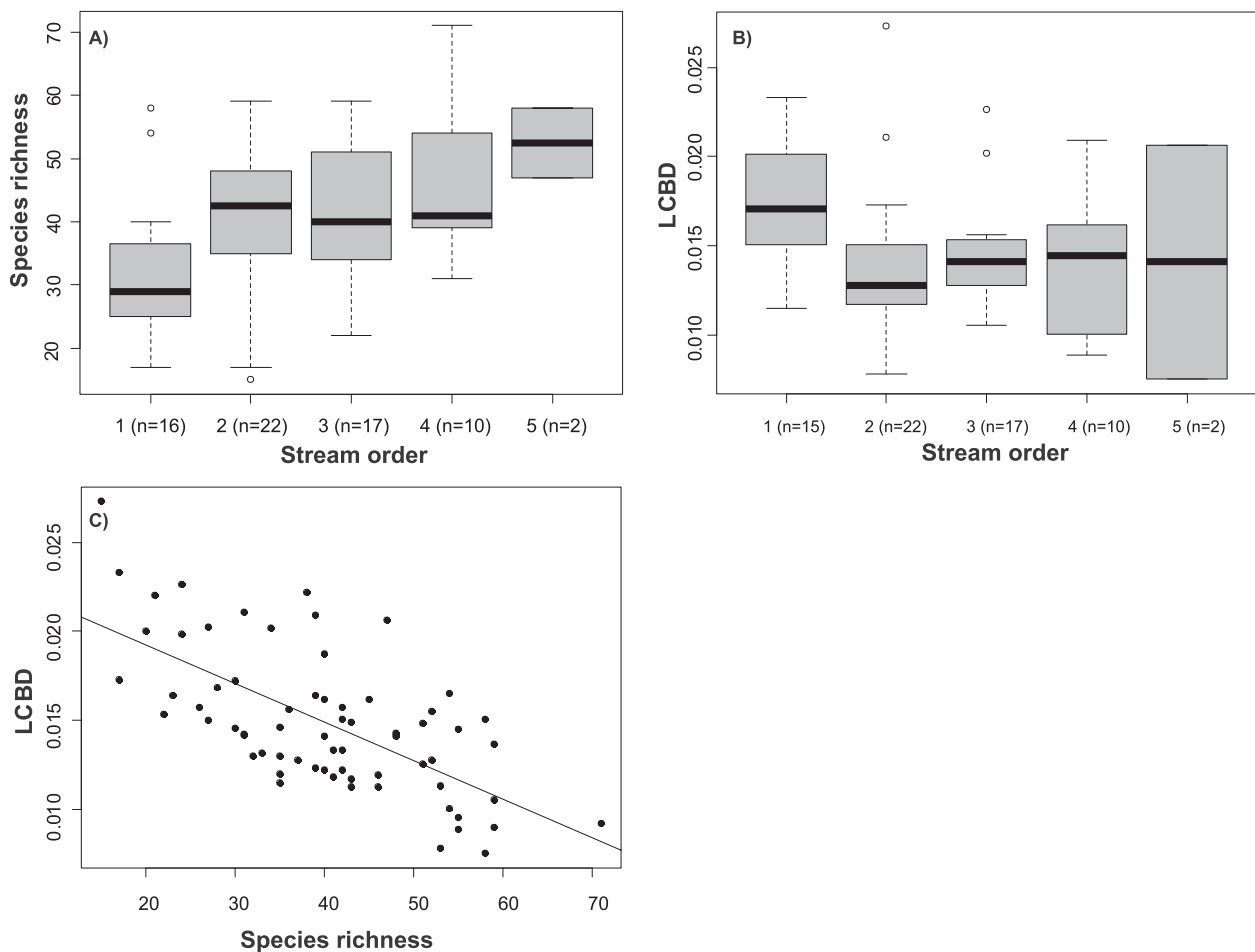
Fig. 3. Boxplots representing the relationship between (A) species richness and (B) LCBD values and stream orders. Also shown is (C) the linear relationship between LCBD and species richness. Abbreviations: LCBD (local contribution to beta diversity).

Our results are congruent with previous studies suggesting that diatom communities are shaped by both environmental and spatial factors (Gothe et al., 2013; Heino et al., 2012; Heino et al., 2014; Potapova and Charles, 2002; Soininen et al., 2016; Verleyen et al., 2009) indicating both environmental control and dispersal limitation (Q_2). However, it cannot be excluded that the observed spatial structure here was caused by mass effects (i.e. due to high dispersal rates, a species can be present also in unfavourable sites (Shmida and Wilson, 1985)) rather than dispersal limitation, due to the relatively small spatial scale (i.e. < 100 km) of the study and high connectivity among sites (Astorga et al., 2012). In such conditions, a mass effect may be caused by the downstream drift of diatom cells (Gothe et al., 2013).

Among local factors, our study highlighted the importance of water pH and conductivity for diatoms. Conductivity (Astorga et al., 2012; Bere and Tundisi, 2011; Biggs, 1995) and water pH (Bere and Tundisi, 2011; Soininen et al., 2004; Telford et al., 2006) have been repeatedly found to be important controlling factors for diatoms also earlier in a wide range of study regions, suggesting that these water chemistry factors are important for diatoms both in tropical and boreal regions. In addition, shading proved to be another important variable structuring diatom communities, a finding, that is further supported by Carpenter and Waite (2000), for example. Thus, although water chemistry plays an indisputable part in structuring diatom communities, it seems that also physical variables may be important, especially light conditions and the substrate of the stream bed. As similar findings emerged in the boreal region as well (Jyrkankallio-Mikkola et al., 2016, 2017), the importance of physical variables in structuring diatom communities applies also to the tropics, which could be important to take into

account in biomonitoring.

As expected, land use affected diatom communities indirectly through water chemistry (Q_2) and our results suggest that forested high elevation sites including montane cloud forests harbored different diatom communities compared with those found at sites with high conductivity. Similar findings have also been reported by Carpenter and Waite (2000). Thus, including land use variables when unravelling factors controlling the diatom communities may be useful, since this approach provides long-term information about the surrounding habitat in addition to snapshot proximate controlling factors, i.e. water chemistry (Bere and Tundisi, 2011; Jyrkankallio-Mikkola et al., 2017). This finding also emphasizes the importance of montane cloud forests for regional aquatic diversity, and furthermore their conservational importance in general as they are of great importance to regional tree diversity, for example in the Taita Hills (Aerts et al., 2011; Schafer et al., 2016) and are currently the most threatened and one of the least studied tropical ecosystems (Williams-Linera, 2002).

The low explanatory power of direct ordination analyses such as RDA used here is common in microbial studies (Beisner et al., 2006; Heino et al., 2012; Nabout et al., 2009). This might be related to some unmeasured environmental variables, although we find this explanation unlikely, since probably the most influential factors structuring diatom communities were included in the analyses. However, we admit that the inclusion of phosphorus might have increased the explanatory power of the model. The surprisingly low phosphorus levels observed might be related to the fact that phosphorus is a major limiting nutrient in old tropical soils (Reich and Oleksyn, 2004) and hence subsequent leaching to the streams may be very low. The low explanatory power
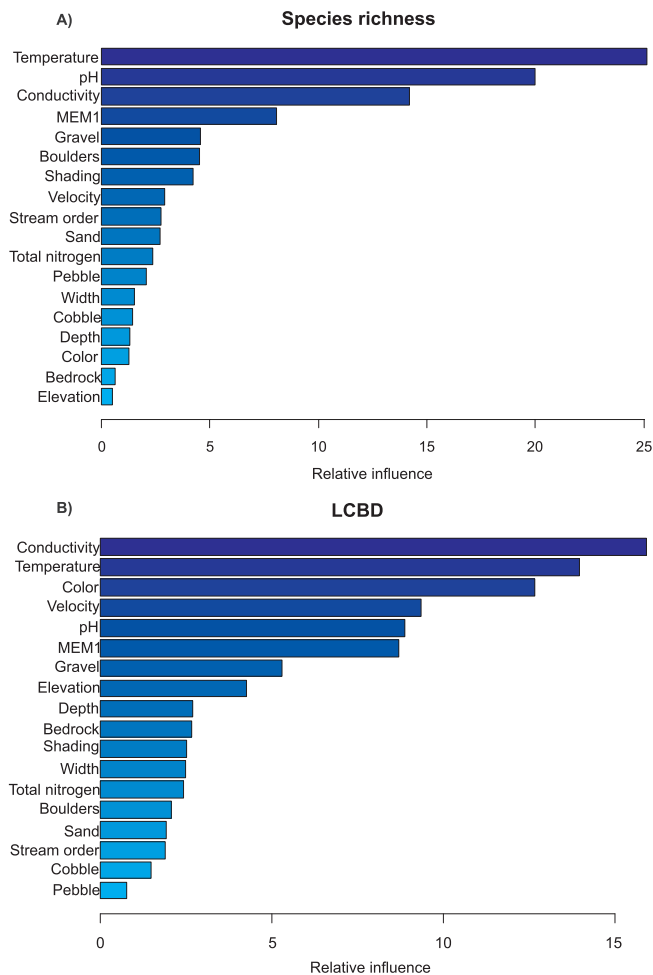
Fig. 4. Boosted regression tree summary showing the relative importance of each variable and related fitted function curves for the four most important variables on (A) species richness and (B) LCBD values. Abbreviations: LCBD (local contribution to beta diversity), MEM1 (spatial eigenvector derived from distance-based Morańs eigenvector maps).

Fig. 5. Boxplots representing the relationship of mean distances from group centroids and stream order based on tests of homogeneity of dispersion analysis. Shown are diatom community compositional data using presence/absence and Sørensen dissimilarity (A) and environmental data using Euclidean distance (B).

might also be due to snap-shot measurements of the local environmental variables, which may not have reflected the prevailing environmental conditions well enough. Indeed, the preceding amount of precipitation may have had an effect on flow conditions and, subsequently, on the diatom community composition. Community assembly mechanisms might also vary, for example, between generalists and specialists, which may hinder the interpretation of environmental and community relationships (Lindstrom and Langenheder, 2012).

As hypothesized, diatom species richness increased with stream order, which is also supported by previous diatom studies (Q3; Sherwood et al., 2000; Stenger-Kovacs et al., 2014). Due to the lack of stream sites above order 5, we cannot rule out the possible decrease in species richness in very large streams and thus the predicted unimodal pattern of species richness along the river network (RCC theory). However, even if headwater streams harboured lower species richness they comprised more unique communities than higher order stream sites (Q$_3$). Headwater streams can be regarded as isolated and less connected habitats compared with downstream sites and hence, the connectivity of the sampling sites may have a strong effect on the community composition via the exchange of individuals (Lopes et al., 2014). A high uniqueness of headwater assemblages have also been reported for macroinvertebrates (Finn et al., 2011), fish (Paller, 1994) and biofilm assemblages (Besemer et al., 2013), stressing the conservational importance of headwater streams, contributing strongly to regional gamma and beta diversity. Our results provide evidence that
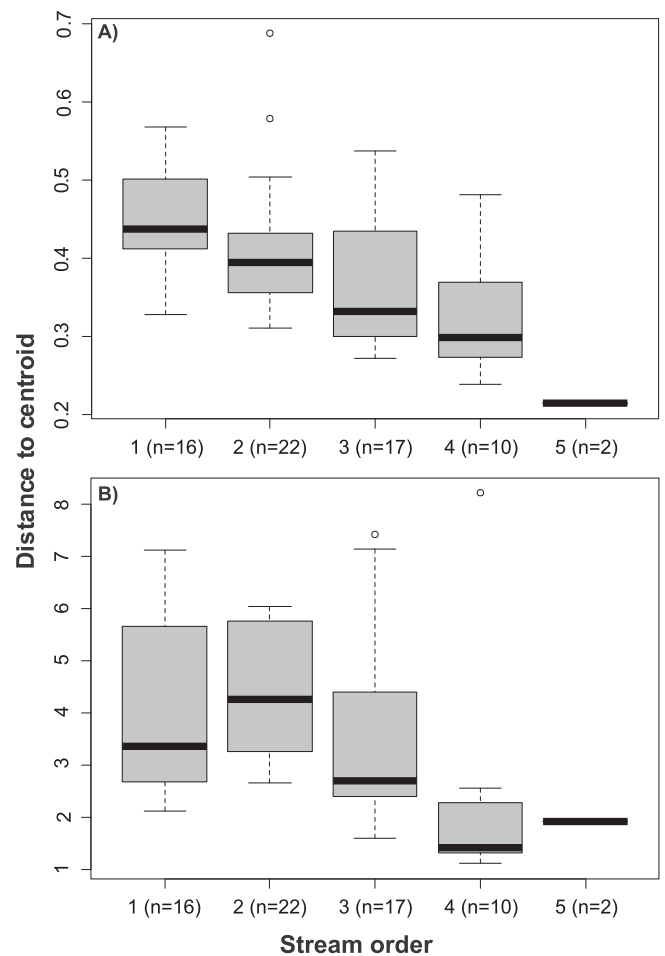
the high uniqueness of headwater communities prevails also in the tropics, perhaps indicating that there are certain general rules for predicting biodiversity (Finn et al., 2011). This result is especially important in areas, where major changes in land use occur together with climate change and consequent droughts may deteriorate or even destroy fragile and important ecosystems such as montane forests. We note that our results are in contrast to the RCC view of headwaters harbouring communities less important for stream biodiversity, and hence we think that our results are also important for stream ecology in general.

In agreement with our findings, a similar negative pattern between community uniqueness and species richness across sites has also been found in several biomes and for different organisms; tropical Brazil for dung beetles (da Silva and Hernandez, 2014), subtropical China for plants (Qiao et al., 2015), temperate France for phytoplankton (Maloufi et al., 2016) and boreal Sweden for macroinvertebrates (Heino et al., 2017). Although Legendre and De Caceres (2013) point out that this negative relationship is not general or obligatory (see paper supporting this view for bacteria in the Canadian subarctic by Comte et al., 2016), it seems to be a relatively common phenomenon at least. Furthermore, this finding suggests that species richness may not be the only or even the best diversity measure for conservational efforts (Dormann et al., 2007), whereas community uniqueness might be in some circumstances more effective in this regard. We thus think that the combination of different metrics would probably be the most informative approach in

many ecosystems.

Of beta diversity components, species turnover was dominant, whereas nestedness was notably smaller. Similar results have been reported also by Wetzel et al. (2012) and Piano et al. (2017). In our study, it is probable that the high number of singletons contributed to the high turnover rate among sites, while richness differences had a smaller influence. Total beta diversity and species turnover were higher in headwater streams, whereas the nestedness component increased downstream, as we expected. This finding may suggest that the increase of anthropogenic influence downstream changes also the relative effects of mechanisms contributing to beta diversity, thus supporting the results of Gutierrez-Canovas et al. (2013). Whereas conductivity, temperature and pH were included into the top five most significant variables affecting species richness and LCBD, stream order played a minor role (Q_4). As BRT analysis takes into account interaction effects between variables, this finding suggests that conductivity, pH and water temperature were among the proximate factors causing the differences in diatom community composition between stream orders, as all these variables showed a significant positive relationship with stream order (Appendix- F in the Supplementary Material). Thus, this finding is congruent with Stenger-Kovacs et al. (2014) who suggested that the stream order may act as a useful parameter summarizing the physical habitat in streams.

As hypothesized, diatom beta diversity and environmental heterogeneity were higher in headwater streams than in larger stream sites (Q_5). Thus, our results provided evidence that along with a stronger dispersal limitation in headwaters, environmental heterogeneity may have promoted variation in diatom community composition in headwaters, suggesting that decreasing environmental heterogeneity downstream may at least partly cause a subsequent decrease in diatom beta diversity towards larger streams. The higher environmental heterogeneity in headwater streams stresses their conservational importance for regional diversity, which gets support from other studies that have found higher habitat heterogeneity to increase beta diversity for planktonic diatoms (Zorzal-Almeida et al., 2017) and phytoplankton in general (Maloufi et al., 2016). Although we admit that the conservation of microbial organisms may not have as strong a research need as the conservation of larger taxa, similar results have also been reported for stream macroinvertebrates (Astorga et al., 2014), emphasizing the effect of environmental heterogeneity on regional diversity. Consequently, strong emphasis should be placed on headwater stream conservation and management in general.

5. Conclusions

Our results indicate that tropical streams do not seem to harbour more diatom species compared with boreal streams. Studies aiming to unravel the determinants of diatom communities are encouraged to consider spatial, land use and physical variables in addition to water chemistry variables. Land use variables may affect diatom communities indirectly through water chemistry and can provide long-term information about the surrounding habitat. Diatom species richness and the uniqueness of the communities may vary across stream orders, with headwater sites encompassing more unique communities and higher order streams, higher species richness. This result is important to take into consideration in biomonitoring and studies focusing on stream diatom species richness and community composition. Environmental heterogeneity seems to be higher in headwater streams and also related to the degree of diatom beta diversity and, thus, our results emphasize the management and conservational importance of headwater streams.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2018.07.030.

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